

Mate guarding and other aspects of reproductive behaviour in *Petalura gigantea* (Odonata: Petaluridae)

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Territorial behaviour and mate guarding are important components of mating systems in various insect groups, including the Odonata. This paper reports observations of male territorial behaviour associated with potential ovipositing sites, and postcopulatory, non-contact mate guarding in *Petalura gigantea*. This is the first unambiguous and detailed report of mate guarding in the Petaluridae. Additional observations of previously undocumented aspects of reproductive behaviour are also reported. These observations are compared with other petalurids.

Keywords: *Petalura gigantea*; Odonata; Petaluridae; dragonflies; copulation; postcopulatory; mate guarding; territorial behaviour; ovipositing; density dependence; reproductive behaviour

Introduction

Male territoriality associated with potential ovipositing sites and postcopulatory mate guarding of females by males are fundamental components in many insect mating systems, including odonates. Mate guarding includes contact and non-contact forms. Its primary purpose is to prevent females from acquiring sperm from rival males (Alcock, 1994; Corbet, 1999). In contact mate guarding, following copulation in the typical wheel position, male Odonata use their specialised anal appendages to maintain a grasp on the female's head or prothorax in the tandem position (Figure 1), while the female oviposits. In extreme cases of contact guarding, male zygopterans may hold ovipositing females underwater. In non-contact guarding, pairs separate following copulation, with the male remaining near the female during any postcopulatory resting period and at least some of the subsequent ovipositing bout, protecting his investment by repulsing rival males (Corbet, 1999). Male territoriality and mate guarding, in the context of the evolution of mating systems, has been, and continues to be, a subject of much interest (e.g. Alcock, 1994; Anholt, 2008; Conrad & Pritchard, 1992; Emlen & Oring, 1977; Ide & Konodoh, 2000), with different classifications of odonate mating systems proposed (e.g. Conrad & Pritchard, 1992; Corbet, 1999; Emlen & Oring, 1977). In odonate species which exhibit mate guarding there is often intra-specific variability in guarding behaviour, depending on frequency of interference by conspecific males. The majority of studies on the subject have focused on the Zygoptera, where mate guarding is widely observed (see Corbet, 1999). Fincke, Waage, and Koenig (1997, p. 70) noted that "Less amenable to study are the more wide-ranging and

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Figure 1. *Petalura gigantea* in the tandem position perched in a fire-killed shrub in a Blue Mountains Sedge Swamp. This pair had been disturbed while perched in copula and flew to a new perch site in tandem, but had not as yet returned to the wheel position to continue mating. This is not a case of postcopulatory, contact mate guarding. Note the damaged forewings on the female (below). 26 January 2008 (photo by Ian Baird).

strong-flying anisopterans such as the Aeshnidae, Cordulegastridae, Gomphidae, Libellulidae and Petaluridae . . . These families . . . represent important gaps in our perspectives on odonate mating patterns and are in need of more study.”

The extant Petaluridae consists of five genera with 11 species currently recognised worldwide, including the endemic Australian genus *Petalura* Leach with five species (Schorr & Paulson, 2014; Theischinger & Endersby, 2009). With the exception of observations of copulation and oviposition there have been few detailed reports of other aspects of reproductive behaviour, such as mate guarding, in petalurids. Based upon limited observation, Tillyard (1909) reported that *Petalura gigantea* Leach males do not guard females. Rowe (1987) also noted that *Uropetala* Selys females oviposit alone. In an observation which suggests mate guarding, Williamson (1901) reported a male *Tachopteryx thoreyi* Hagen “ . . . either fluttering about or resting on a large boulder close at hand” while a female rested in the grass during an ovipositing bout. Davies (1998) also reported a male *P. hesperia* Watson “hanging around” a female as she stopped repeatedly on the surface of potential ovipositing habitat, and then following her at high speed as she flew off down a stream. In a novel observation involving *Tanypteryx hageni* (Selys), C. Beatty (personal communication, 21 July 2014) encountered a tandem pair ovipositing. “I don’t know if the male may have seized her during oviposition (so she may not have actually mated with him and simply abided his presence while she oviposited) but they remained perched together vertically on vegetation while she oviposited, and continued to do so for some time.” No other observations of even possible mate guarding behaviour have previously been reported in the Petaluridae as far as the author is aware.

Although Taketo (1960) described male territoriality, mating and oviposition in *Tanypteryx pryeri* Selys, he did not report mate guarding; instead, after mating while perched in trees, the female separates from the male and proceeds to the nearby oviposition site where she oviposits alone. He also observed no interference with ovipositing females by males. Svhla (1984) similarly reported that even when *T. hageni* males were numerous at a seepage breeding site,

ovipositing females seemed to be ignored by males, although in a single case a male grasped an ovipositing female in tandem. Clement and Meyer (1980) reported that, in general, mated *T. hageni* females are able to enter a site and oviposit amongst the ground-layer vegetation without interference. When ovipositing females were interfered with by males they were grasped in tandem and departed the breeding site to copulate in adjoining forest. Clement and Meyer (1980) also noted a degree of temporal segregation of mating and oviposition, with females usually able to oviposit without interference during late afternoon. No guarding behaviour was reported. The author has also observed a *T. hageni* ovipositing unattended, although territorial males were present within view in the fen breeding site. Territorial males frequently perch on fallen branches, logs and vertical tree trunks within and adjoining their mire breeding sites.

Observations of male territoriality have previously been reported for *T. thoreyi* (Barlow, 1993; Dunkle, 1981; Walker & Smentowski, 2003), *Tanypteryx hageni* (Clement & Meyer, 1980; Svhla, 1959), *T. pryeri* (Taketo, 1960) and both *Uropetala* spp. (Orr, 1994; Rowe, 1987). Interestingly, Rowe (1987) reported that *U. carovei* (White) and *U. chiltonii* Tillyard males demonstrate different territorial behaviours, with *U. chiltonii* spending most of the time perched, interrupted by occasional short flights to defend a territory, compared to *U. carovei* which utilises regular patrol flights of potential breeding habitat. It is noteworthy that these two species reportedly reproduce in different types of habitats, with *U. chiltonii* associated with discrete tussock seepage and bog patches with similarities to the breeding habitats of *P. gigantea* (see Baird, 2012, ch. 6), and *U. carovei* utilising suitable habitat adjoining small streams and along seepage-fed drainages within forested areas (see Rowe, 1987). Rowe (1987) also stated that *U. carovei* males “patrol beats at the edge of scrub or forest country that contains breeding sites”, repeating the same circuit at regular intervals. Taketo (1960) noted that male territoriality in *T. pryeri* served a reproductive function, which is also evident in both *Uropetala* spp. In addition to this function, Clement and Meyer (1980) suggested that observed aggressive territoriality towards nonconspecific odonates by *T. hageni* also functions to reduce competition in their restricted mire habitats. Barrett (1996) referred to “territorial males” in *P. hesperia*, but gave no details of any specific observations. Davies (1998) noted that in a “good” *P. hesperia* colony, 20 or more males may be seen on a suitable day, but that females are rarely seen, and only then in pairs with males. Davies (1998) made no reference to territoriality in this species. In the only other report of territorial behaviour in *Petalura*, G. Theischinger (personal communication, 23 May 2014) observed three males of *P. litorea* Theischinger attacking each other several times, apparently competing for a sunny spot on a barbed wire fence adjacent to breeding habitat. No females were observed. With the exception of ovipositing, aspects of reproductive behaviour, such as male territoriality in association with potential ovipositing sites, have not been described in the non-fossiliferous *Phenes raptor* Rambur (for review, see Baird, 2013).

Dunkle (1981) reported that males of the other non-fossiliferous petalurid, *T. thoreyi*, were territorial when associated with seeps within forest areas where there was strong competition for sun spots for basking. In these cases, territory holders vigorously defended these territories from intruder males, although there was no day-to-day territorial fidelity. However, Dunkle (1981) also observed that, alternatively, *T. thoreyi* males actively and systematically searched the sunny sides of a linear sequence of tree trunks near seeps, putatively for perched females, not prey. Interestingly, Barlow (1991) reported consistently non-aggressive behaviour between *T. thoreyi* males flying and foraging above a pond. Subsequently, Barlow (1993) reported aggressive clashes between males competing for limited basking sites, consistent with the observations by Dunkle (1981), and Walker and Smentowski (2003) noted that sometimes males would chase each other over a fen breeding site.

Davies (1998) reported behaviours of males and females of the huge tropical petalurid, *Petalura ingentissima* Tillyard, which suggested that males are not territorial. “Males and females are rarely seen together and males only rarely along the creeks where the oviposition

sites are located . . . they search the forests for each other . . . ” The only reported observations of reproductive behaviour in the other tropical species, *P. pulcherrima* Tillyard, were by S. Butler and G. Theischinger (Theischinger & Endersby, 2009, p. 250), who noted apparent ovipositing along margins of a *Pandanus* swamp, before 9 a.m. “Males appeared somewhat later, usually when at least a large part of the swamp was sunlit. They mostly settled on dry branches between 1 and 2 m from the ground, probably watching out for arriving or passing females. Copulation was observed late morning and early afternoon again 1 to 2 m from the ground on *Pandanus*”. In a recent note, G. Theischinger (personal communication, 23 May 2014) added that “Females were then not noticed in the habitat except for one that came to the site and went down apparently to oviposit after male activity had ceased.” Exuviae of this species have also been observed in swampy patches along creek banks, where adults were occasionally present (Theischinger & Endersby, 2009, p. 250), also suggesting possible male territorial behaviour.

This paper reports previously undocumented aspects of reproductive behaviour in *P. gigantea*, with the objectives of better understanding the behavioural ecology of this species and mating strategies within the Petaluridae.

Methods

Observations of mate guarding and other aspects of reproductive behaviour in *Petalura gigantea* were made in the Blue Mountains region, New South Wales, Australia (150°20' E, 33°40' S) between November 2003 and February 2010 during fieldwork for a larger, landscape-scale, population study (Baird, 2012, ch. 7). In addition to surveys for exuviae (Baird & Burgin, 2013), this study primarily involved modified ‘Pollard Walk’ transects through the species’ mire habitats documenting relative abundance of imagoes associated primarily with identified potential reproductive habitat. Due to the constraints of the walking transect protocols it was not possible to dedicate excessive time for observation of reproductive behaviour. All observations of mate guarding were recorded.

Results

In addition to weekly imago surveys across the duration of a flying season in six mire patches, 374 annual walking transect surveys were undertaken in 111 mire patches where the species was recorded in at least one of seven survey years. The species was not recorded in 44% of those annual surveys, and only 72 annual surveys recorded more than five adult males. All surveys except two recorded more males than females; the two exceptions were surveys with a very low total observed number of adults. This stands in contrast to the documented sex ratio at emergence, which shows a significant bias in favour of females, confirming that surviving females generally spend their time in non-mire habitat, except for reproductive purposes (Baird, 2012, ch. 7.3; Baird & Burgin, 2013). Of the 210 annual surveys where *Petalura gigantea* was recorded, males were recorded in 209, although only 100 involved sightings of females. Of these 100 surveys, 51 recorded an adult sex ratio ($\sigma:\varphi$) of less than 5:1. Throughout these surveys, 25 unambiguous observations of postcopulatory, non-contact mate guarding were recorded. Guarding behaviour immediately followed copulation during a postcopulatory resting period (see Corbet, 1999) and/or during at least part of the subsequent ovipositing bout. Only three of these included observation of the end of the copulation period. Most observations were made in mire patches where large emergence events had occurred that season. They were characterised by a relatively high abundance of territorial males and by a greater likelihood of females entering the site for mating and oviposition.

Male territoriality

Petalura gigantea is an obligate, groundwater dependent, mire-dwelling species. Suitable seepage habitat is distributed patchily amongst a matrix of unsuitable habitat within individual mires. The proportion of individual mires that provide suitable reproductive habitat is highly variable, spatially and temporally, and may range from a single seepage line in a large mire complex (< 2%) to > 50% of the mire area. Potential habitat for oviposition and larval burrow establishment is characterised by the presence of some emergent seepage water, or at the least, by a moist to saturated, organic-rich substrate (Baird, 2012, ch. 6; 2014; Baird & Burgin, 2013; Benson & Baird, 2012). Within or immediately adjoining breeding habitat, males generally exhibit territorial behaviour, returning to perch in between any conspecific interactions or brief foraging flights, in a manner similar to that reported in *Uropetala chiltonii* (Rowe, 1987). The species exhibits typical percher behaviour, generally perching on graminoids (usually robust sedges) in sedgeland, on shrubs, or occasionally on large fallen branches within their mire habitat. Perch height is generally < 1.2 m above ground level in sedgeland vegetation, reflecting the upper height of the dominant stratum. During windy conditions males may select several potential sedge stem perches before finding one which provides the necessary stability. Scattered shrubs which protrude above the surrounding sedgeland vegetation are generally favoured as perch sites (mostly < 1.8 m above ground level), where available, presumably to provide greater visibility and stability, with individuals using both vertical stems and branches. On a number of occasions territorial males flew up and either investigated and departed, or perched on the author in various positions, including the face. On another occasion, a perched male flew at, and grappled aggressively with, a tiny southern emu-wren, *Stipiturus malachurus* (Maluridae), which had perched several metres away in a shrub while foraging. The wren immediately flew off and the *Petalura* returned to its perch. While perched, both sexes adjust their orientation to the sun to thermoregulate, as reported in other petalurids. Territorial males typically catch flying prey while in mire habitat, returning to perch to consume it, as occurs in *Tachopteryx thoreyi* (Dunkle, 1981), *Tanypteryx hageni* (Clement & Meyer, 1980) and *P. litorea* Theischinger (I.R.C. Baird, unpublished observations), for example.

Based on qualitative observation, male territoriality appears to be somewhat density dependent, increasing in frequency of interactions, and to some extent, decreasing in territory area with increasing male density, at least under some circumstances. Males tend to respond to any movement by conspecifics (in addition to nonconspecifics and other insects in flight), generally taking flight from a perched position and flying at any individual that has entered their territory. Generally, territorial interactions do not involve aggressive contact and grappling, with one individual flying off when confronted by another, although exceptions involving aggressive contact are not unusual.

A small number of observations (over short periods) were made of an unusually high density aggregation of territorial males in small, high quality seepage patches within larger, heterogeneous mire complexes. These involved up to five individuals with < 3 m between any individual. In these atypical cases, the greater proximity of males had resulted in an associated reduction in territory size, and although the frequency of male interactions increased, the flight distance and duration of each interaction before returning to perch had decreased. It is possible that, in addition to the presence of a small patch of high quality seepage habitat, conspecific attraction had drawn these males together to establish a high density aggregation of territory holders, at least temporarily. Due to survey time constraints, no quantitative data are available in relation to these observations. The unusual aspect of these cases was that, elsewhere across the mire, territorial males were distributed at more typical spacing in association with apparently high quality potential ovipositing habitat.

Unless there is strong competition for territories, males tend to space themselves no closer than about 10 m apart in more open sedgeland vegetation, presumably reducing the energetic cost of more frequent interactions. Larger territory sizes may also increase the likelihood of encountering a female entering the site for mating purposes. At high male densities, in particular, resident territory holders may be displaced, at least temporarily, by adjoining territory holders or newcomers in a continuously varying dynamic which may involve frequent perch changes and territory adjustments. Such a dynamic is similar to that reported in *T. hageni* (Clement & Meyer, 1980) and *T. pryeri* (Taketo, 1960). In one small mire, where a large emergence event was recorded in one year, but where there was limited high quality ovipositing habitat and thus potential male territories, the limited territorial male carrying capacity resulted in dispersal of many males (in addition to females) to other mire patches in the local patch network (see Baird, 2012, ch. 7.3.6, 7.4.7).

At low male density, the situation is very different. In one instance, only a single male was observed in a large, high quality mire patch for a month early in the flying season. What was presumed to be the same individual was located during nominally weekly surveys perched in the same shrub or one within several metres of it, suggesting a high level of fidelity to a particular territory in that case. Similar observations of apparent territorial fidelity to a small area, over periods of weeks, were observed in other instances in large mires with relatively low male densities. None of these observations involved marked individuals.

At low male density, particularly later in the flying season, males may utilise a more wide-ranging mate seeking behaviour. This behaviour is characterised by relatively rapid patrol flights along drainage lines through mire patches, presumably to maximise chances of intercepting any female which has entered the breeding habitat for mating purposes. In one instance, the author observed a male, which was apparently following connected streams which drained two separate mire patches within a forest matrix, to establish a patrol area which included both patches. No other male was recorded in either of these patches at that time (see Baird, 2012, ch. 7.4.7). Some apparently non-territorial males also intercept females around mire margins before they are able to enter the breeding habitat and the domain of resident male territory holders. This behaviour was observed in association with high quality breeding sites with a high density of territorial males. It may indicate a particular strategy by non-territorial males or be an opportunistic response by males foraging in adjoining non-mire habitat or around mire margins.

Copulation

Initial tandem formation may occur through interception of a female in flight, but females are often initially grasped while ovipositing or perched. In the latter cases, once tandem formation occurs, they usually take flight. These flights are usually of short duration, and often low altitude flight (frequently < 2 m above ground, depending on vegetation height) above the vegetation within the mire habitat. If the female is receptive to the male, the pair usually moves quickly into the wheel position (Figure 2). There is no courtship. If females are not receptive, they sometimes turn down their abdomen while also attempting to escape by flying off rapidly. The pair perch promptly once in copula, and sometimes beforehand. Often, this involves more than one attempt, as the male tests potential perch supports for stability. In a small number of cases, unguarded females were grabbed by a male in the tandem position between ovipositing bouts, but refused to be dragged away by the male. In one such case, a female was observed tenaciously gripping sedge stems while the male with similar tenacity attempted to remove her while in tandem. When accosted by multiple males, females were observed on a number of occasions departing the mire habitat at speed to escape their unwanted attention. In some cases, these were females disturbed during an ovipositing bout. In most observed cases of ovipositing, no guarding males



Figure 2. *Petalura gigantea* in copula perched in a fire-killed shrub in a Blue Mountains Sedge Swamp with second male perched above. The second male showed no interest in interfering with the mating pair in this case. 5 January 2007 (photo by Ian Baird).

were identified. It is possible that, at times, such aggressive interference was responsible for females flying to a nearby mire patch or seepage where they may complete oviposition with no guarding male, assuming they are not intercepted and re-mated by another male.

Typically, *P. gigantea* perch in sedges or shrubs while in copula, usually within their mire habitat. Exceptionally, however, individuals meet and subsequently mate in non-mire habitats, particularly where those habitats are near mire patches where large emergence events have occurred that season and the likelihood of encountering mates in nearby non-mire habitat is increased accordingly. Only two such matings were observed. No observations of postcopulatory movements of pairs which had mated in non-mire habitat were made. On several occasions copulating pairs perched on the author. Perch height during copulation within breeding habitat may vary from near ground level in sedgeland vegetation, to at least 2 m in taller swamp scrub. Lower perch heights, which may be less conspicuous, are often preferred. Perch height selection is also affected by prevailing wind conditions, with pairs tending to perch lower amongst sedge tussocks at higher wind speeds. Activity of adults, including all aspects of reproductive behaviour, can be observed throughout most of the day under suitable weather conditions at temperatures $> 18^{\circ}\text{C}$. Pairs in copula have been observed as early as 9 a.m. solar time and probably also mate earlier during hot weather, with ovipositing observed into the late afternoon. In addition to males, females are occasionally observed perched in shrubs, in and adjoining mire breeding sites during wet weather and at night and are thus potentially available to mate early in the day under suitable weather conditions. In one case, a male and a female with wet wings were recorded early in the morning after rain, perched 20 cm apart in a shrub in breeding habitat where they presumably spent the night.

Copulation duration may be long, in one case extending for 57 minutes (personal observation), and in another, a little over 2 h (C. Ireland, personal communication, 10 January 2004). In the latter case, the long duration may have been, to some extent, in response to disturbance by the observer, resulting in the pair moving location a number of times in copula. A long copulation period exceeding 20 minutes has also been reported in *Uropetala* (see Rowe, 1987). In some cases, when disturbed by other males, perched pairs in copula will fly off in copula to escape interference; they may relocate within the mire, or leave the breeding habitat and perch in adjoining woodland or other non-mire habitat. Where pairs in copula are disturbed and leave the mire habitat, they may fly upwards and perch higher in the canopy of trees in adjoining woodland, as occurs in *Tanypteryx* spp. (see Clement & Meyer, 1980; Taketo, 1960). In some cases, interference may result in the pair temporarily shifting to the tandem position while in flight, before returning to the wheel position once interference has ceased. Triple connections involving a pair in copula with a second attached male were observed on various occasions in mires with high male density (also see Theischinger, 1975). This often resulted in these groups becoming entangled temporarily amongst dense sedgeland vegetation or falling to the ground in gaps between sedge tussocks. Such interference sometimes resulted in the mating pair departing the breeding site flying in tandem or in copula. In none of these observed cases of interference was the mating pair separated (also see Tillyard, 1909).

Postcopulatory resting phase

Following copulation, the female separates from the male and usually either perches adjacent to the perched male or flutters a short distance to perch in close proximity to the male, either on the same perch or a nearby one (Figure 3). In all three observed cases, in the absence of disturbance by another male, this distance varied between 10 cm and 1 m. In this position, females typically



Figure 3. Postcopulatory non-contact mate guarding by ♂ *Petalura gigantea* perched above the ♀ in resprouting razor sedge, *Lepidosperma limicola*, during the postcopulatory resting period. Despite a deformed abdomen the ♀ successfully copulated. The saturated soft peaty substrate around the edges of the shallow, seepage-filled depression at the base of sedge tussocks provided suitable potential ovipositing sites. 12 months post-fire in a Blue Mountains Sedge Swamp. 28 November 2007 (photo by Ian Baird).

rest for a period before fluttering a short distance to access the ground surface to investigate suitable substrate for ovipositing. This postcopulatory resting phase varied in duration, in one instance lasting for c.30 minutes, but in the other observed instances was < 5 minutes. In the longer instance, it is possible that observer disturbance was responsible for the extended duration of the resting phase. Females can be reluctant to commence or continue ovipositing in the presence of an observer who is too close, and caution is needed in making and interpreting such observations. In cases where copulation had occurred in breeding habitat and was not affected by interference by other males, the distance between the copulatory or postcopulatory resting perch and the initial oviposition site was < 3 m, and frequently much less.

Oviposition

Oviposition is endosubstratic (Matushkina & Klass, 2011), as with other petalurids (for reviews, see Baird, 2012, pp. 30–31; 2013), and involves insertion of the ovipositor, and sometimes distal abdominal segments, into some form of moist or saturated, organic-rich soil substrate, into fissures in the substrate, or amongst or under live or decomposing plant material overlying the substrate, including graminoids, *Sphagnum*, roots and litter. No females were observed ovipositing into substrate covered by more than 1–2 mm of water. Whenever females were observed lowering themselves backwards through sedgeland foliage to access the substrate for ovipositing, but instead encountered a pool of water in an inter-tussock depression, they discontinued when the distal segments of their abdomen were immersed in water. See Baird (2012, pp. 212–215, 236–238) for details of microhabitat attributes of ovipositing sites and photographs of females ovipositing in various microhabitats. In one instance, a female attempted to oviposit into the author's muddy footwear.

Postcopulatory mate guarding

During the postcopulatory resting phase, in the absence of interference by other males, guarding males may remain perched or briefly take flight on one or more occasion, and then relocate to the same or another perch in close proximity to the perched female. Whenever a second male flies in to investigate the perched female or the male, guarding males typically take flight immediately and repulse the intruder, chasing him away before returning promptly to near the female. Such activity usually does not involve aggressive grappling contact between males, with most intruders departing without resistance. On one occasion, after a long postcopulatory resting period of c.30 minutes, the male took flight from his nearby guarding perch and flew at the female, repeatedly making light contact, possibly attempting, in this case unsuccessfully, to encourage her to leave her resting perch and commence oviposition. This was the only observation of this behaviour. While guarding, males may demonstrate considerable restlessness.

In the great majority of ovipositing females observed by the author there was no apparent guarding male. When mate guarding was observed, once the female had commenced investigating a substrate for ovipositing or was engaged in ovipositing, males generally remained within several metres of the female, and often much less (Figure 4), at least initially repulsing any males which entered their guarding space. In some ambiguous cases, a male was initially observed in open sedgeland habitat perched further than this from an ovipositing female, but was conjectured to be still engaged in guarding behaviour, albeit perhaps somewhat less committed. The duration of guarding by, and fidelity of males once ovipositing has commenced, is highly variable, apparently increasing with higher male density. In high quality breeding habitat with a high male density any male flights tend to attract interference, thus increasing frequency of interactions between the guarding male and adjoining territory holders. In one instance, in habitat with a very



Figure 4. Postcopulatory non-contact mate guarding by ♂ *Petalura gigantea* perched on a burnt shrub stem in a resprouting Blue Mountains Sedge Swamp, post-fire, with ♀ ovipositing in saturated, fire-scorched, peaty substrate c.60 cm away. 5 January 2007 (photo by Ian Baird).

low male density, a male guarding an ovipositing female (Figure 4) repulsed the first intruder male, but failed to return to guarding behaviour after chasing him away. In other instances, males were observed chasing several consecutive intruder males away from their guarding space before returning to assume a perched guarding position. During this time the female might relocate at least once following a short ovipositing bout to investigate another ovipositing site in close proximity, typically within several metres, but often much less. In high quality sites, females often only flutter to the next inter-tussock gap in the sedgeland vegetation to recommence ovipositing; during these short flights, they may be exposed to potential interference from other males. Once on the substrate, particularly in dense sedgeland vegetation, however, they may be relatively well concealed from such interference. Females typically spend a number of minutes at a particular location probing the substrate with their abdomen, testing for suitability and engaging in oviposition before relocating, in a similar manner to that of *U. chiltonii* in bog tussock habitat (Wolfe, 1953). Females arch and move their abdomens frequently as they investigate the substrate and oviposit, and may vibrate their wings at the same time. The longest ovipositing bout observed was almost one hour, during which the female moved location frequently, usually a short distance. In this case, ovipositing was unguarded after the guarding male failed to return from chasing away the first intruder male. After almost an hour, the female was apparently spotted by a male, who grasped her in tandem and flew off rapidly.

Discussion

The unambiguous observations of postcopulatory, non-contact mate guarding in *Petalura gigantea* documented in this study appear to be the first such reported for any petalurid, with the exception of single observations of apparent guarding behaviour in *Tachopteryx thoreyi* (Williamson, 1901) and *P. hesperia* (Davies, 1998). The novel observation of a female *Tanypeteryx hageni*

ovipositing while in tandem with a male (C. Beatty, personal communication, 21 July 2014) is anomalous and cannot be assumed to represent an unusual case of postcopulatory, contact mate guarding. With the exception of copulation and ovipositing behaviour (e.g. Baird, 2012; Davies, 1998; Dearson, 1999; Theischinger & Endersby, 2009; Tillyard, 1909), an unpublished observation of territorial behaviour in *P. litorea* (G. Theischinger, personal communication, 23 May 2014), and an observation of apparent male territoriality associated with ovipositing sites in *P. pulcherrima* (Theischinger & Endersby, 2009), the observations of other aspects of reproductive behaviour, including male territoriality, are also the first reported for any *Petalura* sp. The maximum copulation duration reported for *P. gigantea* is the longest reported for any petalurid and there have been no previous accounts of postcopulatory resting phase duration for petalurids as far as the author is aware. The maximum durations for those behaviours observed in *P. gigantea* in this study are higher than for most, but not all odonates as reported by Corbet (1999).

Observations of territorial behaviour by male *P. gigantea* in mire habitats are broadly consistent with those reported for other petalurids with patchily distributed mire or seepage breeding habitats: *P. litorea* (G. Theischinger, personal communication, 23 May 2014), *T. thoreyi* (Dunkle, 1981), *Tanypteryx hageni* (Clement & Meyer, 1980; Svhla, 1959), *T. pryeri* (Taketo, 1960) and *Uropetala chiltonii* (Rowe, 1987). In contrast to the observation of male territoriality in *T. thoreyi* (Dunkle, 1981), however, which was associated with limited sun-spot basking sites in or adjoining potential seepage ovipositing habitat, mire habitats of *P. gigantea* are generally not sun limited. Territoriality in this species is directly associated with potential ovipositing sites, serving a primarily reproductive purpose, as in *Tanypteryx* and *Uropetala* spp. Although Davies (1998) did not report territoriality in *P. hesperia*, it is probable that males of this species demonstrate territoriality in their swamp habitat in a similar manner to *P. gigantea*, although it is possible that it may also be associated with basking sites within that habitat, depending upon the openness or canopy cover of the vegetation. The reference to “territorial males” in *P. hesperia* (Barrett, 1996) and the apparent case of guarding behaviour (Davies, 1998) are consistent with this. In a recent study in an isolated mire patch on the north coast of New South Wales, with vegetation structure similar to habitats used by *P. gigantea*, the author also observed aspects of reproductive behaviour in *P. litorea*, including copulation, oviposition, male territoriality and probable mate guarding (unpublished observations). All of these behaviours were consistent with those reported here for *P. gigantea*.

Petalurids such as *P. gigantea*, which are associated with discrete mire reproductive habitat patches distributed within a matrix of non-reproductive habitat, are generally characterised by male territoriality in such habitat, and in some species at least, by postcopulatory mate guarding. As in the case of *P. gigantea*, both of these features of the mating strategy in other petalurids can be expected to be density dependent, where they occur, and vary in relation to the characteristics of their reproductive habitat, such as habitat quality and area. Such patterns have been reported elsewhere in the Odonata (Corbet, 1999). Interestingly, although both *Tanypteryx* spp. reproduce in patchily distributed mire or seepage habitats where territorial behaviour by males has been documented, males of neither of these relatively small petalurids appear to guard their mates (but note the anomalous observation by C. Beatty of a female *T. hageni* ovipositing in the tandem position). In both species, pairs in copula have been reported departing the breeding site to perch in adjoining trees, with the female subsequently returning to the breeding site to oviposit unattended. This is in contrast to *P. gigantea*, which, in the absence of interference by other males, usually copulates within the mire breeding habitats where tandem formation occurs, and practices mate guarding, albeit variably. The mating strategy of *U. chiltonii*, however, appears to differ from *P. gigantea* and both *Tanypteryx* spp. Although this species is reported to practise male territoriality, and usually copulate within or adjoining its seepage breeding sites where tandem formation occurs, mate guarding has not been reported (see Rowe, 1987; Wolfe, 1953).

Variation in reproductive strategies has been reported between *Uropetala* spp., with Rowe (1987) noting that they are characterised by divergent male territorial behaviours in association with their different types of breeding habitat; namely, percher-type territory defence in discrete tussock seepages and bog patches (*U. chiltonii*), or regular patrol flights of potential ovipositing habitat along seepage-fed drainages and stream edges (more linear habitats) in forested areas (*U. carovei*). The reproductive strategies in the two tropical petalurids, *P. ingentissima* and *P. pulcherrima*, might also vary in relation to their reproductive habitats. These habitats include soft saturated soils associated with seepage on edges of small streams or swampy patches adjoining streams in forested areas (“rainforest for *P. ingentissima*, monsoon forest for *P. pulcherrima*”; G. Theischinger, personal communication, 30 May 2014) in both species (Davies, 1998; Theischinger & Endersby, 2009), and larger and more open swamp patches, at least in the case of *P. pulcherrima* (Theischinger & Endersby, 2009, p. 250). The differences between these reproductive habitats mirror to some extent the different reproductive habitats reportedly used by the two *Uropetala* spp. (Rowe, 1987). Davies (1998) suggested that *P. ingentissima* probably utilises opportunistic mate meeting and more wide-ranging movements in primarily forest habitats, while observations of *P. pulcherrima* (Theischinger & Endersby, 2009, p. 250) also suggest male territoriality and mate meeting in association with larger and more open swamp patches, where they occur, in addition to swampy patches along stream edges in forested areas. The use of sunny forest openings, vehicle tracks and an anthropogenic meadow above a forest stream by adult *P. ingentissima*, has also been reported (e.g. Davies, 1998; Silsby, 1994). These observations appear to have been associated primarily with sunny sites, but potential ovipositing habitat, such as a stream edge, was located nearby in one case (Silsby, 1994), suggesting possible male territorial behaviour if the observed individuals were male. Rapid and powerful flights by *P. ingentissima* were reported in these instances, and in the Silsby (1994) observation, individuals flew up to investigate the observers and then flew off, repeating the performance on three visits by observers. Similar behaviour by territorial males of *P. gigantea* and *P. litorea* in their mire habitats has frequently been observed by the author.

Based upon its reported range of reproductive habitats in small seeps or boggy stream margins in mostly forested areas (e.g. Baird, 2013; Fleck, 2011; Svhla, 1960) and in moist rainforest ground litter (Garrison & Muzón, 1995), and upon the observed behaviours of adults (for review, see Baird, 2013), *Phenes raptor* may also demonstrate flexibility in reproductive strategies depending on the type of reproductive habitat. Individuals of unknown sex have been observed repeatedly returning to small sunny openings in forest areas for foraging purposes, repeating the same route over a period of three days (Svhla, 1960). Similar use of sunny forest openings for foraging and basking has been reported by G. Jurzitz (R. Andress, personal communication, 5 September 2011), who observed *Phenes* using open areas “at the edge of swampy land along a stream” and in a clearing about 20 m above a fast running, mountain river (also see Joseph, 1929; Jurzitz, 1989). Baird (2013) reported similar use of such forest openings; while these sightings were not associated directly with identified potential ovipositing habitat, such habitat was either locally available or within 50 m. This included a tentative identification of a *Phenes* flying rapidly along a sunny forest trail past a small seepage where a *Phenes* larva was subsequently recorded. A *Phenes* imago was also caught near a shallow riffle where a larva was collected, which was also near where Garrison and Muzón (1995) found larvae in moist rainforest ground litter (R. Garrison, personal communication, 18 April 2013). Ray Andress (personal communication, 14 June, 2011) has noted that, behaviourally, *Ph. raptor* appears more similar to aeshnid than percher-type petalurids, such as *P. gigantea*.

Additional observations will be necessary to better understand reproductive strategies, and the relationship between them and the different reproductive habitats used in petalurids, particularly *Ph. raptor*, *P. ingentissima*, *P. pulcherrima* and *Uropetala* spp. The observations of mate guarding and other aspects of reproductive behaviour in *P. gigantea* reported here will contribute to

better understanding the behavioural ecology of the species and the factors responsible for the variability in mating strategies within the Petaluridae. While more detailed quantitative study of reproductive behaviour in *P. gigantea* would be useful, opportunities are constrained by the unpredictable and highly variable nature of emergence events in individual mire patches in particular years (Baird, 2012, ch. 7.4.7), and the expected limitations of the mark-release-recapture technique, for this species in this environment.

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